METHOD OF STUDYING THE BIOLOGICAL CYCLE OF ELEMENTS IN FOREST

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The biological cycle of elements under the forest canopy is a complex, many-sided process. To encompass all its aspects in a single study is doubtless tempting, but very difficult to accomplish. The investigation should be developed in successive stages.

In a series of investigations on the biological cycle of elements undertaken by the Faculty of Soil Science at Moscow University, the first stage was the examination of the annual cycles in the overall cycle (1944-1951). The task at this stage was to determine by direct chemical analysis of plants the amount of principal nutrients which the forest, as a result of the annual cycle, extracts from the soil, retains in the developing stand, and returns to the soil as litter and dead wood. The establishment of experiments in plantations of various age classes made it possible to determine the characteristics of the long-term cycles.

A general summary of results of this first stage of investigation was given in a paper at the All-Union Conference of Soil Scientists in January-February 1956 (12) and at the Sixth International Congress of Soil Science Society in Paris in the same year (32).

A. F. Tyulin (17, 18, 19) made a counter-proposal to the method used by our Faculty in the first stage of our investigations of the biological cycle. His method was based on soil analyses which indicated that in forest soils of Tellermanov area, the total nitrogen content fluctuated considerably throughout the growing season. Tyulin attributed these fluctuations to nitrogen consumption by the root systems of the oak forest which resulted in decreased amounts of nitrogen in the soil, and to secretion of nitrogen from the roots which increased the nitrogen content in the soil. On the basis of these indirect data, Tyulin concluded that the consumption of nutrients by an oak forest must be approximately ten times as great as that established by direct plant analysis reported by our Faculty.

The inaccuracy of Tyulin's approach to the determination of nutrient consumption of a forest was so obvious that it seemed unnecessary to explain it in print. However, in 1958 Vinokurov and Tyurmenko (5) published a paper recommending Tyulin's approach unreservedly. Therefore, it became necessary to explain the inaccuracy of his method of studying the biological cycle.

The change in total nitrogen content of soil beneath a forest during the growing season was known from Tyulin's work and there was no reason to doubt it. Long-term data on the dynamics of the total nitrogen content of forest soils were published by Feher in 1929-1936 (26, 27, 28). Our Faculty obtained similar results, except that they indicated more precisely (Table 1) that the considerable amount of fluctuation in nitrogen content is observed in the richer soils and that in poorer soils, the nitrogen content remains fairly constant.

Before Tyulin's work, none of those who observed the changes in total nitrogen content of forest soils attributed them, either wholly or mainly, to uptake and secretion of nitrogen by the tree root systems. If we represent the soil as a sterile medium devoid of microorganisms and soil-litter fauna, then changes in total nitrogen content of this hypothetical soil could be attributed only to the action of root systems. However, such an assumption is not applicable to the actual soil, which is the habitat not only for root systems of the higher plants but also for algae, fungi, actinomycetes, bacteria and a varied fauna.

Oligonitrophylous organisms in great quanti-

[1] Vinokurov, M.A. and A.N. Tyurmenko. 1958. Data on the biological cycle of nitrogen and phosphorus in forest. Pochvovedeniye No. 7.

Table 1

Dynamics of total nitrogen content (%) in soils of oak stand on the Voronezh State Forest, 1953
(Research by E. M. Shmurova)

Soil	Months						
	April	May	June	July	Aug.	Sept.	Oct.
Dark gray-brown forest, sandy loam	0. 26	0. 34	0. 23	0. 22	0. 29	0. 29	0. 29
Gray-brown forest, loam	0. 22	0. 26	0. 23	0. 22	0. 24	0. 23	0. 23
Brown forest sand	0. 15	0. 18	0. 13	0. 14	0. 14	0. 14	0. 13
Light-brown forest sand	0. 11	0. 11	0. 09	0. 11	0. 11	0. 11	0. 11

ties enrich forest soils with fixed nitrogen. A similar influence is exerted by nodule bacteria on the roots of astragalus, vetchling (lathyrus), vetch (vica) and other forest leguminous plants. In deciduous forest soils possessing a nitrifying capacity, the activity of those denitrifyers which reduce nitrates to elementary nitrogen contributes to nitrogen loss. The possibility of partial losses of ammonia formed during ammonification and denitrification is not excluded. The intake by soil of nitrogen and other elements during the process of decomposition of dead vegetation must be considered.

A substantial effect on the chemical composition of the humus-accumulating layer and on its nitrogen and phosphorus content is produced by soil-litter fauna. They intermix this layer with the forest litter, and with the underlying horizons, thereby enriching it in nitrogen and phosphorus, thus decreasing the latter's nitrogen, phosphorus, sulphur, calcium, etc. content. In addition, the fauna introduce nitrogen and other elements into the soil with their excreta and, at the end of their life-cycle, with their dead bodies. The life-span of some is very short.

The activity of both microorganisms and soil-litter fauna has its own seasonal character, so that they may cause regular seasonal changes in soil properties. Feher (27) showed, with a wealth of data, the decrease in numbers and activity of the microflora during the summer drying of forest soils. This was observed in our investigations, too. Zrazhevskii (8) describes the decrease in activity of earthworms and certain other soil fauna during a period of sharp decrease in soil moisture. He also shows that excessive moisture, which impedes soil aeration, has an adverse effect on soil fauna.

The effect of atmospheric precipitation, which controls the movement of soluble compounds of nitrogen and other elements from the forest litter to the humus-accumulation horizon -- and when the fall is greater it is deeper -- should be taken into account. In the ensuing drying period, the soluble compounds rise from deeper layers.

To disregard the effect of microorganism activity and soil fauna on the dynamics of nutrients in forest soils is without doubt a major fundamental error. Variations in the total nutrient content of forest soils depend on many factors, which effects have not been studied from the quantitative viewpoint. It is inadmissible arbitrarily to ascribe all changes, wholly or mainly, to the activity of the roots alone, in the total absence of direct data as to the amount of nitrogen and other elements secreted by the roots of trees.

To demonstrate that all fluctuations in nitrogen content of the soil depend solely on root activity, the following single experiment was presented (19, p. 277). An area of 4 m^2 was completely cleared of forest litter, then the soil was removed to a depth of 20 cm. All visible roots were carefully extracted from the soil. Next, the soil was placed in another previously-prepared hollow, having corresponding dimensions. After this treatment the total nitrogen content of the soil remained almost constant (0. 05%-0. 55%).

Results of the experiment cannot be accepted as convincing. The upper part of the humus-accumulation layer of dark-gray forest clay loams, to a depth of 20 cm, are very highly interwoven with roots of trees, shrubs, and coarse woodland grasses. The removal of the entire root mass from almost a cubic meter (0. 8) of earth involves long and laborious work which inevitably has an effect on the soil fauna. During the sifting of a soil mass of this kind every creature that can jump, crawl or fly left it. Moreover, the removal of roots disturbed the activity of rhizospheric microorganisms, especially bacteria, which utilize the

organic compounds secreted from roots as a source of energy. The soil obtained was devoid of roots and improverished to a considerable degree of living organisms.

It is not surprising that a method based on disregard of the part played by the microflora and fauna in forest soils led to a paradoxical representation of the nitrogen cycle. Thus, for a 50-year-old oak plantation a value of 1.5 metric tons/ha nitrogen consumption by the forest was found, according to the difference between the highest and lowest total nitrogen content of the soil. According to our data, based on analysis of the tree itself, it was only 0.15 metric tons/ha. On this basis it was concluded that all data for nitrogen consumption by the forest obtained by our Faculty were approximately 10 times too low (17, p. 109). This leads to the following conclusions: a 12-year-old oak stand, according to our data, takes up 29 kg/ha of nitrogen annually from the soil; multiplying this by 10 gives 290 kg/ha, although the nitrogen content of the entire stand is only 172 kg/ha. According to our data, when 20-25 years old the stand absorbs 130 kg/ha; multiplying this value by ten gives 1300 kg/ha, but the total nitrogen content of the stand is 500-550 kg/ha. It follows that the stand annually takes up more nitrogen from the soil than it contains. From the physiological aspect the absorption and secretion of such large amounts of nitrogen through the root system remained unexplained.

In another paper (5) it was stated that a 45- to 55-year-old basswood stand takes 825 kg/ha of nitrogen from the soil. According to our Faculty's data a 40-year-old basswood stand absorbs 73 kg/ha from the soil, and the entire stand, including undergrowth, contains only 703 kg/ha of nitrogen (13).

Supporters of this method of studying the biological cycle are inclined to apply it to other elements as well. In the paper by Vinokurov and Tyurmenko the phosphorus consumption of a 45- to 55-year-old basswood stand is determined in this way as 130 kg/ha P_2O_5, while the content of the entire stand is about 150 kg/ha. The very high P_2O_5 content in leaves (about 2%) and roots (about 0.5%) of the basswood is surprising. Other authors give considerably lower values.

In the polemic papers under consideration two further objections to the method used by our Faculty were advanced. The first consists of an assertion that the study of the amount of elements taken up by the forest from the soil and partly restored to it later through litter and dead wood represents a revival of the agronomic theory of removal and return (17). The second is that we studied the biological cycle by chemical analysis of felled, not living trees (5, 17).

The consumption by forest of nutrients from the soil and the restoration to the soil of part of them with litter and dead wood represents an objective natural phenomenon existing independently of ourselves. They bear no relation of any kind to the man-made agronomic theory of the artificial restoration to the soil with fertilizers of nutrients removed with crops. With reference to the chemical analysis of felled trees -- to determine the mass of the tree, including its root system, and to perform a total chemical analysis of a living tree is impossible. The total content of nitrogen and ash elements in the leaves, branches, trunk and roots of a tree will not change when it is felled. The critics of my work quote in their papers data of chemical analysis of leaves and roots, not only dead but further treated with hot steam.

The method of studying the biological cycle of elements by means of soil analysis cannot be accepted since it has no theoretical basis and leads to improbable data. There remains the direct plant-analysis method used by our Faculty. This method in principle fully answers the purpose indicated, which does not exclude the possibility of improving it in detail. By this means the annual and long-term minor cycles within the general biological cycle are considered. Further, sub-annual cycles exist whose duration is measured in shorter divisions of time. Another method of approach is necessary to study these. One of the chief characteristics of sub-annual cycles is that the same amount of nutrients can be taken up from the soil by plants and returned to it again many times during a year.

In 1952 our investigations were concerned chiefly with seasonal changes in the chemical composition of the soil and plants. The results appeared in a series of publications (1, 2, 14, 15, 16, 20, 21). In this paper it is necessary to deal in detail with the seasonal changes in the chemical composition of various parts of the tree. To clarify this question, representative trees, two at a time, were taken at the Voronezh National Forest three times in the growing season (spring, summer and autumn) on the same experimental area in a 50-year-old oak plantation. The mass of leaves, branches, trunk and roots was determined and a chemical analysis made of them.

The most substantial variations (Table 2) in the content of the elements studied were found in the leaves and, to a lesser degree, in the branches. From spring to autumn the content of nitrogen, potassium and to a lesser extent, of magnesium in the leaves consistently decreased. The content of silica, calcium and iron, on the other hand, increased towards autumn. These changes were smaller in branches than in leaves. Analysis of the trunk and roots revealed no substantial sub-annual changes in the

Table 2

Content of nitrogen and ash elements in various parts of oak (Site quality III), 1957
(Research by L. G. Bogashova)

Part of tree	Sampling date	Content as % of dry matter (100° C)							
		N	Si	Fe	Ca	Mg	K	P	Total
Leaves	June 10	3,30	0,79	0,01	0,57	0,09	2,34	0,32	7,42
	August 13	2,47	2,23	0,02	1,01	0,08	1,95	0,20	8,96
	Sept. 30	1,97	4,10	0,03	1,17	0,06	1.78	0,32	9,43
Branches	June 30	1,02	0,37	0,01	0,72	0,06	0,96	0,13	3,27
	August 13	0,72	0,40	0,01	1,03	0,05	0,74	0,11	3,06
	Sept. 30	0,70	0,51	0,01	1,05	0,05	0,35	0,07	2,74
Trunk	June 10	0,24	0,05	0,01	0,23	0,04	0,13	0,03	0,73
	July 13	0,24	0,05	0,01	0,21	0,03	0,11	0,02	0,67
	Sept. 30	0,20	0,06	0,02	0,37	0,02	0,11	0,02	0,80
Roots	June 10	0,60	1,06	0,04	0,84	0,08	0,65	0,16	3,43
	July 13	0,62	0,42	0,03	0,98	0,08	0,59	0,10	2,81
	Sept. 30	0,54	1,06	0,03	1,05	0,05	0,48	0,10	3,31

Note: Comma represents decimal point.

content of the majority of elements.

The data obtained show to satisfactory conclusions that the oak's maximum consumption of nitrogen, potassium, magnesium and phosphorus occurred in June. In July there was a considerable decrease in the nitrogen and potassium content. Since the sum of the elements in the leaves increases from June to September, the increase in silica and calcium content was not just relative. The accumulation of these elements in the leaf continues throughout the growing period.

The decrease in nitrogen and potassium content in the leaves and branches was not accompanied by a change in their percentage content in the trunk and roots. The question arises as to the course followed by the nitrogen and potassium lost by the leaves and branches.

According to Raskatov's research (11) carried out in the oak plantations of the Voronezh National Forest, the greatest increment in mass of oaks takes place from June to July; it decreases somewhat in August, mostly (4%-8% of the annual growth) in September. According to our Faculty's data, the annual growth of an oak stand (50 years old, site quality III) contains (in kg/ha): N, 19; Ca, 27; K, 8; Mg, less than 3; sulphur, about 2; remaining elements, <1. The mass of leaves in these oak plantations is 1. 3 metric tons/ha (as dry matter at 100° C), and of branches 0. 86 metric tons/ha. A decrease in the nitrogen content of leaves from 3. 30% to 1. 97% gives a nitrogen loss of 17. 3 kg/ha from the leaves, and a decrease in potassium content from 2. 34% to 1. 78% gives a potassium loss of 7. 3 kg/ha. The total loss from leaves and branches is: nitrogen 17. 6 and potassium 7. 8 kg/ha. These values correspond closely to the amount of these elements used for annual growth. Similar results were obtained for magnesium.

The increase in calcium content in all parts of the tree from May to September, with a considerably simultaneous use for growth (27 kg/ha), confirms its accumulation in the oak stand throughout the growing period. The calculations given convince one that the decrease in nitrogen and potassium content of leaves and branches towards autumn cannot be regarded as evidence of their secretion into the soil in large quantities. This does not exclude secretion in small quantities of some elements by roots into the soil.

In studying root secretion considerable difficulties were encountered. The following temporary method was used: one of the secondary roots of the tree, 30-40 cm long, was dug up, cleaned of soil and subsequently immersed in distilled water. To secure aeration, air was bubbled through for five days. Observations showed that under these conditions the root not only lived but even grew. The interation of roots with water in experiments made in 1956 and 1957 was observed for about a month, after which the

water was changed.[2] Experiments were made on roots of oak, pine and spruce. In the first half of the summer no secretions perceptible by analysis were detected; in August secretions of small quantities of K, Ca, Al and P were noted. Potassium secretion amounted to 1 mg/l as K_2O alumina 0.12-0.24 mg/l Al_2O_3.

In order to exclude inequality of ion concentrations in the cell sap and the solution, experiments were conducted substituting nutrient solutions of salts for distilled water. By this means it was possible to obtain clearer results. For instance, it was possible to show that in the first half of the summer an absorption of K_2O of 41 mg/l for pine and 50 mg/l for oak took place from a solution of KNO_3 (200 mg/l), while in August the K_2O content in the pots increased up to 52 mg/l in the experiment with oak and up to 47 mg/l in that with pine. These studies confirmed the presence of root secretion into the soil of some elements in the autumn (Studies by E. M. Boriskina-Samoilova). Unfortunately, with the method employed it was not possible to judge the amount of these exudations for the entire tree.

An hypothesis developed that during prolonged interaction between roots and solution the alternating processes of intake and secretion may compensate for each other. In the summer of 1958, experiments were conducted using the same method with a change of solutions every 12 hours; in the evening (after the day period) and in the morning (after the night period). Twelve hours of interaction between roots and solution was sufficient for the absorption or release into the solution of Ca, Mg and K (Study by N. Titova). Further research in this direction requires improved methods.

Until recently it was widely thought that atmospheric precipitation leaches nitrogen and ash elements only from leaf litter, i. e. from dead leaves. Green leaves hanging on the tree, by the force of turgor, firmly retain these elements. The possibility of leaching of elements from leaves of trees, from bushes and from grass cover was not usually taken into account in explaining the causes leading to change of content of these elements both in leaves and soil. Moreover, the literature contains many indications that atmospheric precipitation leaches many elements from living leaves.

As early as 1804 de Saussure (34) wrote that leaves pass on to rainwater the salts which they contain. In 1883, Councler (24) adduced experimental confirmation of this. He found that the leaves of box elder (Acer negundo) grown under greenhouse conditions, compared to leaves of the same tree grown in the field under the open sky, contained more sulphuric acid (3.90% as against 0.97%), phosphoric acid (2.60% as against 0.46%), potassium (9.67% as against 4.51%) and sodium (0.12% as against 0.09%). He ascribed the lower content of these elements in the leaves of the box elder in the field to leaching by atmospheric precipitation.

Later, Arens (22, 23) wrote of the leaching by rainwater of ash elements from the leaves of trees. According to his observations, a few hours' rainfall may decrease the element content of leaves by 10%-30% and the potassium content by as much as 50%. In one of these investigations, leaves of a beech forest containing 16.2 kg/ha K_2O, lost 9.8 kg/ha after 24 hours of rain. Losses almost as great are observed in five hours of rain.

Arens points out that the ash element content of leaves increases in dry weather and that a fresh rainfall again results in leaching. In the growing season this is repeated frequently and the sum gives a considerable value which describes the intensity of the branch of the biological cycle described.

Arens suggested calling this phenomenon "kuticuläre Exkretion" to differentiate it from leaching of dead leaves.

In this connection the investigations of Lausberg (30) are interesting. From an isolated horse-chestnut tree, he picked off leaves daily at the same hour and analyzed them. The data obtained show a decrease in calcium and potassium content after each rainfall, and a return to the previous level after ensuing dry weather.

Not only rain but also humid mist produced a decrease in the content of these elements.

Tamm (33) carried out more prolonged investigations in 1950 in the environs of Stockholm (Table 3).

Table 3

Leaching of ash elements by rainwater from the crowns of trees (Research by C. O. Tamm)

Site of rainwater collection	Entered the soil from Oct. 19 to Nov. 30 (kg/ha)		
	Ca	K	Na
Open field	0.4	0.3	0.6
Forest clearing	0.5	0.3	0.5
Under spruce	>2.2	>2.4	>3.7
Under pine	2.5	2.7	3.2

[2] The method was described in greater detail in Bogashova's paper (1).

Under spruce the calculation was incomplete, as the funnels used (24 cm in diameter) gave more water than the flasks could hold. The data analyzed (Table 3) show that rainwater leaches a considerable amount of bases from the crowns. Tamm writes that only one-fifth of the total annual precipitation fell during the period of his investigation. The actual annual intake by the soil of nutrients leached by rainwater from leaves is considerably higher. Rainwater leaches more ash elements from deciduous than from coniferous species. Examining rainwater on September 26, 1950, Tamm found calcium (per mg/l): in water from pine forest crowns 4. 0; in water from oak plantations 9. 1; in water from birch plantations, 7. 2; the corresponding figures for potassium were 6. 3, 15. 0, 17. 4, etc.

Investigations carried out in New Zealand by Will (35) in a 30-year-old pine forest (Pinus radiata, D. Don) in 1954-55 (Table 4) are another example.

We must pause again for one important conclusion. In recent times the isotope method has been used for quantitative study of root secretions from trees. The appearance in the soil of P^{32} (or another element), however, introduced under the bark of a tree or on the leaf surface cannot serve to determine the amounts of the element exuded by the roots. Its appearance in the soil may be the result of leaching from the leaves: i. e. of the phenomenon of "cuticular exudation." This was confirmed experimentally in the work of Mes (31).

The last question to be examined concerns the effect exerted on the biological cycle of elements by the dying off, during the tree's life, of part of the tree roots.

Taking fruit trees as an example, Kolesnikov (9) showed that the production of new, and the dying-off of old, root endings and even of entire "root systems" goes on throughout the entire growing season. Great difficul-

Table 4

Intake by pine-forest soil of ash elements from litter and rainwater, November 26, 1954 to June 2, 1955 (Research by G. M. Will)

Place of collection	Precipitation (mm)	Litter (g/m^2)	Entered the soil (mg/m^2)				
			Ca	Mg	K	Na	P
Open area	687	—	1. 3	1. 4	2. 2	23. 4	—
Under pine	420	—	4. 7	12. 6	21. 5	81. 5	4. 9
Pine litter-fall	—	252	61. 6	21. 2	16. 5	10. 4	24. 6

In the moister climate total rainwater leached more potassium from forest crowns than was contained in litter. One cannot agree with Will's proposal to calculate the nutrient intake by the soil from the sum of its content in litter and rainwater. The elements leached from the crowns by rain are absorbed again from the soil by the root systems of trees when dry weather returns. The intake of elements by the soil with rainwater is related to the subannual cycle which is incorrect to include on an equal basis with the litter in the annual cycle.

The sum of elements leached from forest crowns in a year serves as an index for the amount of elements passing through a plant, but not for the requirement of elements for the growth of that plant.

Preliminary experiments carried out in 1958 at the Voronezh National Forest confirmed the considerable extent of leaching of nitrogen, potassium, calcium and phosphorus from leaves in oak and aspen stands (research by I. K. Sviridova).

ties of methodology are encountered when determining the extent of the participation of the dying-off of minute roots and absorbing rootlets. For this purpose, Orlov (10) proposed a method based on selecting, from a soil monolith of 1000 ml volume by means of forceps and needle, a root of <0. 3 mm diameter with subsequent additional examination under a magnifying glass. This work is extremely laborious. Using his method, Orlov concluded that the annual value of dying-off amounts to 0. 6 metric tons/ha. Unfortunately the object of his study was atypical — spruce stands on chernozem.

In 1956, using Orlov's method, a study of the root systems of a 50-year-old oak stand (site quality III) in the Voronezh National Forest was undertaken. The soil samples for this study were taken three times during the season -- in June, July and August, between the 14th and 21st of each month. For the first two months the total mass of living roots of a diameter <0. 3 mm in

the 0-10 layer[3] amounted to 0. 8 metric tons/ha; in August it decreased to 0. 5 metric tons/ha, which indicates a prevalence of dying-off of roots. If one agrees with Orlov's judgement (10), that half of the roots die off, then the proportion which dies off will amount to 0. 4 metric tons/ha, which approximates the decrease of living roots for July to August.

Chemical analysis showed (Table 5) that the percentage of silica, iron, aluminum and potassium in roots increased with a decrease in diameter. There were no regular changes in calcium and magnesium content. The nitrogen content was not determined for technical reasons.

Table 5

Results of the chemical analysis of oak roots of various diameters
(Research by E. M. Boriskina-Smoĭlova)

Root diameter	Content as % of dry matter (100° C)						
	Si	Fe	Al	Ca	Mg	K	P
>7 cm	0. 07	0. 01	0. 14	0. 94	0. 27	0. 40	0. 08
7-0.1 cm	0. 19	0. 04	0. 24	1. 36	0. 30	0. 71	0. 08
1-0.3 mm	0. 52	0. 15	0. 34	0. 56	0. 22	0. 72	0. 08
<0. 3 mm	1. 06	1. 00	0. 83	0. 71	0. 22	4. 16	0. 14

Table 6

Comparison of ash element content in roots having a diameter < 0. 3 mm and in litter (kg/ha)

Content	Si	Fe	Al	Ca	Mg	K	P
In absorbing roots	7. 7	7. 2	6. 0	5. 1	1. 6	8. 3	1. 0
In litter	17. 9	0. 6	2. 1	66. 0	10. 7	15. 8	5. 6

Comparison of the ash element content of this part of the roots with litter per acre (Table 6) shows that considerably more aluminum and iron is retained in the minute roots than in the annual litter on the ground. The considerable silica and potassium content in the roots, amounting to about half the annual intake of these elements with litter, should also be noted. The phosphorus content is relatively small.

Thus, the dying off of roots <0. 3 mm in diameter has a substantial effect on the biological cycle of elements. This effect is particularly clearly shown in the aluminum and iron cycle. Investigations on this aspect continue.

The biological cycle of elements in a forest is a complicated polycyclic process depending on the combination of many factors. A leading part is played by the activity of forest vegetation in conjunction with the soil fauna.

This activity takes place under changing conditions of climate and weather.

Long-term cycles are composed of successive annual cycles. The content of annual cycles

[3] A large proportion of roots of this diameter is contained in the top 5 cm; 1/10 is contained in the 5-10 cm layer and below 20 cm, there are almost none. Lateral roots leading off the large roots head upwards for the humus horizon where they branch off extensively.

varies according to the period of development of the stand (age classes), depending on the increase of nutrient and moisture requirements of forest-forming trees with age, the gradual natural thinning of the stand, variation of light, development of underbrush, soil cover, etc.

The annual minor cycles within the general biological cycle of elements are conditioned by the removal of a specific amount of elements from the soil during growth and by the return to the soil, in the same year, of part of them with litter and dead wood. Here the annual water cycle should also be taken into account.

The work of the Soil Science Faculty of Moscow University was directed primarily towards the study of long-term and annual cycles within the biological cycle of elements. For this purpose a corresponding method of study was evolved which vindicated itself in practice. The lack of agreement in the carbon and oxygen cycle is to be attributed to a defect in the method caused by difficulties in analytical procedure.

The study of sub-annual cycles within the biological cycle is the most complex. Their duration may vary widely; some of the processes vary hour by hour. The sub-annual cycles consist of the appearance and dying-off of bacteria, algae, fungi and a number of microscopic and larger soil fauna, the formation and dying off of root hairs, the synthesis and decomposition of organic matter, the leaching of elements from leaves by rain, dew and mist and their re-absorption by roots, ion exchange processes between plant roots and the soil, and nitrogen fixation and denitrification. Leaching by atmospheric precipitation and capillary rise, etc. have a substantial effect. It is impossible to list all these individual minor cycles. At the second stage of our investigations we began the study of a number of sub-annual cycles. Some of the results obtained are given by way of example.

The method recommended by Vinokurov and others of studying the biological cycle of elements by means of total soil analysis cannot give even an approximate idea of a single minor cycle within the general biological cycle and should, therefore, not be adopted.

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